materially to elucidate the subject of the mode of flow of water round bends in pipes, and the manner in which bends cause augmentation of frictional resistance in pipes, a subject in regard to which I believe no good exposition has hitherto been published in any printed books or papers; but about which various views, mostly crude and misleading, have been published from time to time, and are now often repeated, but which, almost entirely, ought to be at once rejected.

VI. "On the Modification of the Excitability of Motor Nerves produced by Injury"*. By G. J. Romanes, M.A., F.L.S. Communicated by Prof. Sanderson, M.D., F.R.S. Received April 13, 1876.

§ 1. If the gastrocnemius of a frog be placed in a horizontal direction on non-polarizable electrodes with its convex surface uppermost, one may generally observe that the muscle is somewhat more sensitive to minimal stimulation, supplied by *closure* of the constant current, when the femoral end rests on the kathode, than when this end rests on the anode. Conversely, under similar circumstances the gastrocnemius is more sensitive to minimal stimulation, supplied by *opening* of the constant current, when the femoral end rests on the anode, than when this end rests on the kathode. In view of the other facts of electrotonus, the present ones are of interest; because, as the sciatic nerve enters the gastrocnemius near the femoral end of the latter, and then spreads out its peripheral ramifications as it advances, in the experiments just mentioned one electrode is in almost immediate contact with the nerve-trunk where it enters the muscle, while the other electrode supports the part of the muscle that contains only peripheral nervous elements. It is therefore to be expected, upon the theory of electrotonus, that the muscle under these conditions should prove itself most sensitive to the closing shock when the nerve-trunk rests on the kathode, and most sensitive to the opening shock when the nerve-trunk rests on the anode.

It is to be observed, however, that although this expectation is in most cases fulfilled, it is not so invariably. Different gastrocnemius muscles, though treated as far as possible in exactly the same way, manifest considerable differences, both in their general sensitiveness to electrical stimulation, and in their relative sensitiveness to interruptions of the ascending and of the descending currents. Even the same muscle, if rapidly prepared, will generally be found to undergo fluctuations in these respects from minute to minute. Attributing this fact to the unnatural conditions which the experiment imposed on the process of nutrition, I conducted some observations on muscles while they were still attached to the body

* For further details, remarks, statements of methods, &c., see a fuller notice in the forthcoming (July) Number of the 'Journal of Anatomy and Physiology.'

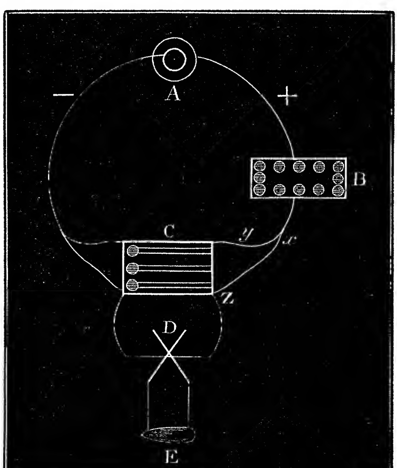
of the frog; but the results yielded by this method were not more uniform than those which I had previously obtained by the method of rapidly preparing and observing excised muscles.

§ 2. If the gastrocnemius of a frog be placed on non-polarizable electrodes in the position already described in § 1, and if care has been taken not to injure the attached sciatic nerve, I find that upon now dividing this nerve, either near or just within the muscle, remarkable alterations ensue, not only, as is already known, in the *general* sensitiveness of the muscle, but also, and more particularly, in its *relative* sensitiveness to make and to break of the current. The following are the mean results yielded by a large number of experiments:—

Descending make		Ascending make		Descending break		Ascending break	
before cutting.	after cutting.	before cutting.	after cutting.	before cutting.	after cutting.	before cutting.	after cutting.
24	27	36	46	2	32	1	$1\frac{1}{2}$

In this Table the word "descending" means passage of the current from the femoral to the tarsal end of the gastrocnemius, and "ascending," of course, passage of the current in the opposite direction. "Cutting" means section of the sciatic nerve just after it enters the muscle; and the numbers represent the relative sensitiveness of the muscle to the stimuli which are indicated above them*. I have appended a diagram (p. 11),

* The numbers are thus obtained:—Suppose A to be the battery, B a set of resistance-coils, C a rheochord, D a commutator, and E the muscle. By removing a plug



from B the resistance is increased, and therefore the current through E is diminished. But the effect of removing a plug from C, although likewise that of increasing the resistance through the whole circuit, is to *augment* the current passing through E. For, previous to removing a plug from C, the current branched at x, and the resistance

which is intended to represent, in a graphic form, the numerical relations set forth in the above Table. In each couplet contained in that diagram the left-hand line represents the sensitiveness of the muscle to the stimulus indicated before cutting, while the right-hand line represents the sensitiveness of the muscle to the same stimulus after cutting. As in the Table, so in the diagram, all the proportions are referred to the ascending break as to a unit—this being the stimulus to which the muscle is least sensitive, and for which, therefore, the strongest current is required in order to elicit a contraction.

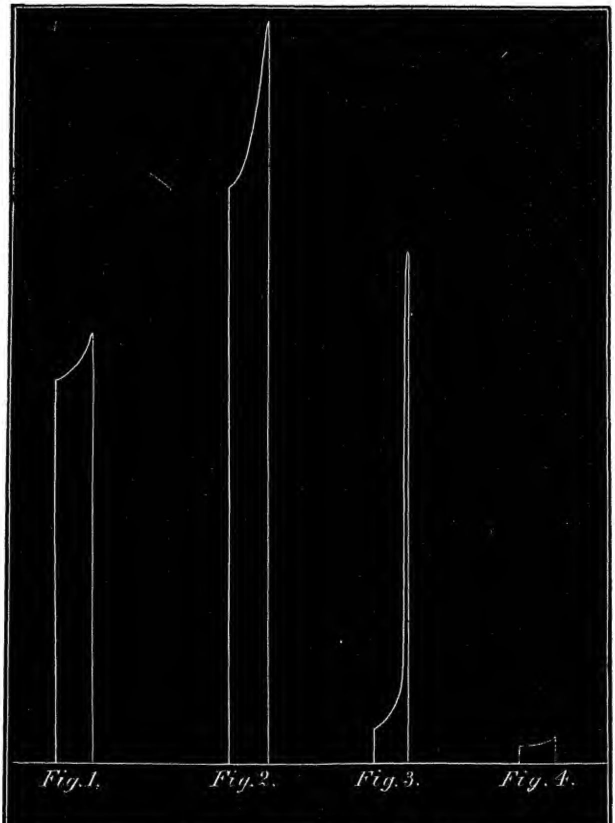
With regard to these results, I may offer the following observations. In the first place, it is evident that the increase of excitability shown by the muscle after cutting is affected to an extraordinary extent by the *direction* of the current; and, further, that the manner in which it is so affected is very instructive when considered in relation to the known facts of electrotonus. For just as before cutting the *normal* sensitiveness of the muscle is greatest to the closing excitation when its femoral end (or nerve-trunk) rests on the kathode, and to the opening excitation when this end rests on the anode, so after the general sensitiveness has been exalted by cutting the *exaltation* shows itself in a far higher degree to the closing excitation when the femoral end (or severed nerve-trunk) rests on the kathode, and to the opening excitation when this end rests on the anode. Thus it is that the curves in figs. 2 and 3 are so much steeper than those in figs. 1 and 4. The only fact, then, that does not seem to admit of any very satisfactory explanation is the altogether *disproportionate* increase of excitability which the muscle after cutting exhibits to the descending break (fig. 3) as compared with the ascending make (fig. 2). This fact, therefore, led to the following experiments.

§ 3. Dr. Burdon Sanderson suggested that if we suppose the breaking excitation to be of a more *instantaneous* nature than the making one, the fact in question might admit of a probable explanation; for in this case the breaking stimulus would bear more resemblance to an induction-shock than would the making stimulus; and as it is well known how sensitive nerve is to the induction-shock, we might reasonably conclude that, when the sensitiveness of the nerve is increased by section, it would

in E being high as compared with that in C, the principal part of the current takes the course x, y, C, A. But if a plug be removed from C, the resistance in C is increased, and a proportional amount of the current takes the direction x, z, E, A. Hence the effect of removing a plug from B is that of diminishing the current in E, while the opposite effect results on removing a plug from C.

Such being the apparatus, in all my experiments I removed one plug from B, and thus worked with a current of constant intensity so far as the whole circuit was concerned. The requisite variations in the intensity of the stimuli were, of course, effected by the rheochord C. Now the numbers in the above Table are obtained by a very simple calculation. Suppose, for instance, that the minimal ascending break contraction requires 18 ohms' resistance to be thrown into the rheochord, while the minimal ascending make only requires ·5 to be thrown in, then the relative sensitiveness of the muscle to the ascending break and make would be approximately represented by the numbers 1 : 36.

probably become more than proportionally increased to the more sudden stimulus. In order to test the correctness of this hypothesis, Dr. Sanderson further suggested that the period of the muscle's latent stimulation before and after cutting should be taken, and also that the following experiment should be tried. By means of an appropriate apparatus,



1. Descending make. 2. Ascending make. 3. Descending break. 4. Ascending break.

the uncut muscle was to have supplied to it a galvanic stimulus of measured duration; and this duration was to be graduated down to the point at which the break succeeded the make with a rapidity just sufficiently great to prevent the muscle from responding to either stimulus. The strength of the current remaining unaltered, the nerve was then to be cut through at the usual place; and, lastly, it was to be observed whether or not the muscle was thus rendered more sensitive to stimuli of short duration. So far as this part of the inquiry has as yet proceeded, the results are as follow.

Section of the nerve (either just above the knee or immediately after

it enters the muscle) is in all cases attended with a marked increase of sensibility to stimuli of short duration; *i. e.* stimuli of much shorter duration are able to evoke responsive contractions in the muscle after cutting than are required to do so before cutting. At first, therefore, it seemed that this experiment was confirmatory of the hypothesis which it was designed to test. This, however, is not so; for it was observed that the increased sensitiveness in question was only shown when the femoral end of the muscle rested on the kathode, while it was scarcely, if at all, apparent when this end rested on the anode. This fact, of course, led to the inference that the augmented excitability to stimuli of short duration had reference, not to the opening, but to the closing excitation. Accordingly I fitted up an appropriate arrangement of wires and keys, by which I could at pleasure throw in ordinary opening and closing excitations, or the closing and opening excitations of short duration. In this way it was easy, by comparing in the two cases the nature of the contractions (which in almost every muscle presents some idiosyncratic differences on make and break), to obtain an optical proof that my inference was correct. The exalted sensitiveness of the muscle after section of its nerve to stimuli of short duration had reference exclusively to the closing excitation.

This fact is of interest in itself, but it fails to answer the question as to why section of a nerve causes so disproportionate an effect on its sensitiveness in the muscle to the excitation which is supplied by the descending break. Nor have I any satisfactory answer to give to this question, unless the following consideration may be deemed so. Before section of the sciatic nerve, the gastrocnemius muscle is immensely more sensitive to the ascending make than to the descending break (figs. 2 and 3, left-hand lines). Consequently, when the general sensitiveness of the nerve is increased by section, the increase has not so much room (so to speak) for its occurrence in the one case as in the other. Seeing that the minimal make contraction occurs at a point so much nearer to zero of the current's intensity than does the minimal break contraction, when both these minimals are reduced still further by nerve-section, the latter minimal has a much wider range through which it is free to fall than has the former. Of course this fact need not prevent the lesser fall from being numerically proportional to the greater one, however small the observed differences may be. The question, however, is as to how far a strictly *numerical* proportion is in this case a fair one. I think we must certainly hold that the value as a stimulus of any given increment of current is determined by the proportion which such increment bears to the intensity of current that is required to produce adequate stimulation. In other words, any given unit of electrical intensity has more influence as an excitant if added to a current of a small number of units (a weak current) than if added to a current of a large number of units (a strong current). But if this is so, it follows that *subtraction* of a unit from a strong current must have less effect than

subtraction of the same unit from a weak current. Now when the general excitability of the muscle is raised by cutting, the effect is that the muscle is able, both in the case of the ascending make and in that of descending break, to afford (as it were) to part with some units of the stimulating influence which were previously required to cause adequate stimulation. Hence, forasmuch as the sum of such units which it had to spare before cutting was so much less in the case of the make than in that of the break, in the case of the make each unit must have been of a correspondingly greater value as a stimulant. Consequently, when both the minimals are reduced by cutting, the reduction may take place in a strictly proportional manner; only, if the proportion has reference to the *value of the electrical units as stimulants*, it follows, from what has been said, that there will probably be no *numerical* proportion between the two ratios.

In favour of this explanation, it is to be remembered that, as already stated, nerve-section produces much more than a proportional effect in the ascending make as compared with the descending break, in respect of increasing the excitability of the muscle *to stimuli of short duration.* It is as though the comparatively small number of units of *electrical intensity* by which the minimal make is diminished through nerve-section represents a great actual increase in excitability, *when this is estimated by some other method*; or, to turn to the diagram, it seems as though the small distance through which the curve in fig. 2 passes as compared with the curve in fig. 3 really represents an increase of excitability much more important than the curve expresses: it seems as though it is just because the difficulty of ascending (so to speak) increases in so rapid a ratio as its curves approach the zero level, that the steep curve of the descending break terminates at, or below, the point where the much less steep curve of the ascending make begins. This appears to be so, because, on testing the increase of excitability by means of stimuli of short duration, it is found that the relatively low curve in fig. 2 represents what would doubtless be a relatively steep curve, if it were possible to institute the numerical comparisons in the case of stimuli of minimal duration, as it is possible to do so in the case of stimuli of minimal intensity.

These remarks, however, are only made by way of suggestion; and I confess that, *à priori*, I should certainly not have expected so great a disproportion to subsist between the curves in figs. 2 and 3.

§ 4. Sometimes severe section of a tolerably well-curarized muscle will be followed by a development of the breaking contraction treated of in § 2. I attribute this fact to incomplete poisoning of the nerve-elements in the muscle; for the following experiments prove conclusively that in an uncurarized muscle the development of the breaking contraction after cutting is a purely nervous effect.

(*a*) Section of the sciatic nerve just above the knee causes all the characteristic alterations in the minimal makes and breaks, and this nearly

as well as does section of the nerve in the muscle. Moreover the higher up the nerve is cut, the less is the degree in which these characteristic alterations occur, until, if the section be made at about the origin of the femur or one third of its length lower down, no trace of these alterations can be detected.

(*b*) Stimulating the sciatic nerve with acids, alkalies, &c., and warming it has the same sort of effects as cutting.

(*c*) Throwing the end of the sciatic nearest the gastrocnemius into kathelectrotonus has a well-marked effect of the same kind; while throwing the same part into anelectrotonus has the opposite effect, though not in so strongly marked a degree.

(*d*) Severe galvanic tetanization of the gastrocnemius is frequently followed by an increase of sensitiveness to the descending break nearly as remarkable as that which follows cutting. As this effect does not seem to occur in well-curarized muscles, I conclude that it must be due to an increase in the excitability of the intramuscular nervous elements through injury.

§ 5. Another method which I employed to test the effects of nerve-section on excitability was one which, in the first instance, I fell upon accidentally. It consisted in joining up the non-polarizable electrodes with a continuous bridge of clay made perfectly flat on its upper surface. Care being taken to keep this surface uniformly moist, the sciatic nerve in a nerve-muscle preparation was laid upon it; so that when the current passed through the clay bridge a portion of it also passed through the sciatic nerve, thereby stimulating the attached muscle. The advantage of this method consists in the facility with which different parts of the nerve-length may be stimulated to the exclusion of other parts. By a curious coincidence, Prof. Rutherford appears to have been working at this subject at about the same time as myself, though quite independently of me. It was only a few days ago that I became aware of this fact by observing an article in this month's Number of the 'Journal of Anatomy and Physiology,' in which Prof. Rutherford states his methods and results. As nearly all the latter agree in every particular with those which I obtained, I am now relieved from the necessity of detailing them. It is desirable, however, to state that, viewed in the light of my other experiments, these results amount to this:—When a few millimetres of nerve-length, including the extreme nerve-section, rested on the clay, a much less strength of current was required to produce the breaking contraction in the muscle than when any other portion of the nerve of equal length was allowed to rest on the clay. That is, in Prof. Rutherford's words, "*the striking fact, however, is that without altering the strength of the current* all the phenomena of Pflüger's law could be obtained by transmitting it through a central, middle, or peripheral portion of nerve, at one time in an ascending, at another time in a descending direction."

It may be worth while to state, as showing the astonishing excitability

of the extreme nerve-section, that if the nerve, while hanging in a vertical direction over the flat surface of the clay bridge, be lowered until the section just touches the flat surface of the clay, it may frequently be observed that the attached muscle responds to make and to break of the current. Yet this must be a case of almost complete transverse stimulation of nerve; for, thinking that there might possibly be some passage of the current from the clay into the nerve in a semilenticular form, I tried a number of times the effect of ligaturing a nerve with a fine human hair, then with a fine pair of scissors making the transverse section as close beneath the ligature as possible, and, lastly, lowering the nerve-section on the clay as before. In no one case, however, did I succeed in obtaining any results similar to those which I obtained with unligatured nerves. It may be stated that in all these experiments with the clay bridge, I graduated the amount of nerve-length to be laid on it by means of a horizontal glass rod firmly fixed to the tube of a microscope. The free end of the rod was pointed, and usually passed between the tendo Achillis and the tibia, the latter having been previously severed at the knee. The sciatic nerve was thus allowed to depend in a vertical direction, and could be very accurately adjusted upon the clay bridge by means of the rack-work which moved the tube of the microscope.

§ 6. During the course of the above investigation concerning the effects of nerve-injury on excitability, several other facts of interest were incidentally observed. It seems desirable, therefore, to add a brief account of these facts.

When an uncurarized muscle is in a state of moderately strong tetanus from the passage of a rather weak galvanic current, it may occasionally be observed that some part or parts of the muscle begin to *pulsate* in a strictly rhythmical manner—the parts concerned alternating their periods of tetanus with periods of repose, sometimes at about the rate which is observable in a frog's lymphatic heart, and sometimes faster. I have counted such pulsations through more than 100 revolutions, without a single intermission and in perfectly regular time throughout. That this interesting phenomenon is exclusively due to the intramuscular nervous element is, I think, proved by the fact that I have never seen it to occur in any one of the hundreds of curarized muscles which I have this year subjected to the influence of the constant current. Moreover, on one occasion I noticed a very good instance of rhythmical pulsation in a partly tetanized gastrocnemius, when I happened to have the attached sciatic on another pair of electrodes. Of course it occurred to me to try the effects of throwing the nerve near the muscle first into anelectrotonus and then into kathelectrotonus. The results were most decided. With a current of properly graduated intensity passing through the gastrocnemius, it was always quite easy to inhibit the pulsating effect in the muscle by throwing the attached nerve into anelectrotonus, while the pulsations were always seen to recommence as soon as the polarizing

current in the nerve was broken. Conversely, if the nerve was thrown into kathelectrotonus, the pulsating effect could be produced in the muscle by a current of less intensity than was required to produce this effect when the nerve was either in anelectrotonus or in the normal state.

§ 7. I have made several experiments with the view of showing the major influence of the kathode on closing, and of the anode on opening, in the case of well-curarized muscle; but on the present occasion it seems unnecessary to describe more than one.

If the curarized sartorius of a frog is placed on non-polarizable electrodes, and is somewhat stretched in a longitudinal direction by means of two weights attached to its two ends, it may almost invariably be observed (especially when the contractions become sluggish by exposure of the muscle) that upon closure of the circuit, and during all the time of its passage, the substance of the muscle *draws* towards the kathode, while on the kathode itself the substance of the muscle heaps up and spreads out in a very beautiful and distinctive manner. On now reversing the current, all the phenomena take place in the reverse way. Hence, by placing any minute body anywhere on the muscle between the poles, this body may be seen to travel some distance towards the kathode every time the current is reversed. Again, if a small transverse incision be made in the muscle anywhere between the poles, it gapes towards the kathode every time the current is reversed. Lastly, if two appropriately weighted levers be attached one to each end of the muscle, when the current is passing in one direction the lever nearest the kathode is raised; whereas when the current is reversed this lever, which is now nearest the anode, falls, while the other lever rises.

§ 8. If the copper wire terminals of a Daniell's element be taken one in each hand, and the strength of the current be graduated down to the point at which minimal stimulation is obtained by placing on a fresh muscle first the anode and then the kathode, it may invariably be observed that if this order is reversed, by first laying on the kathode and then the anode, no contraction will be given unless the strength of the current is somewhat increased. This curious fact may be observed equally well on curarized and on uncurarized muscles. It is independent of the direction of the current, and is not affected either by insulation of the muscle or by placing it on a gas-pipe. The phenomenon is likewise unaffected by placing the anode or the kathode in an unclosed circuit of a Grove's cell upon the muscle, and then experimented with the weakened circuit from the Daniell's cell as before. It may be observed that the long muscles of the thigh, either *in situ* or excised, are best adapted for making these experiments*.

* Until a short time ago I was not aware that any difference had as yet been detected between the effects of anodic and of kathodic closure. My attention, however, has now been directed to the observations of Hitzig, in which he finds that on minimal stimula-

A
−
+
B
C
y
x
D
E

1.	2.	3.	4.
Descending make.	Ascending make.	Descending break.	Ascending break.